GARDEN COMPARISON OF GERMINATION AND SEEDLING GROWTH OF *YUCCA WHIPPLEI* SUBSPECIES (AGAVACEAE)

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ABSTRACT

Subspecies of *Yucca whipplei* represent different life history modes. Subspecies *whipplei* and *parishii* are semelparous, subsp. *caespitosa* is iteroparous, subsp. *percursa* has vegetative reproduction, and subsp. *intermedia* combines both patterns of these last two taxa. Germination of all subspecies was greatly inhibited at 40°C suggesting seedling recruitment is restricted during hotter months. Brief heat treatment at 100°C prior to wetting did not enhance germination, as is the case in many chaparral shrubs commonly associated with *Yucca.* Rather, germination was reduced at this temperature, though the reduction was least for the two semelparous forms most commonly associated with chaparral. Seedling biomass after four months in a common environment showed highly significant differences among subspecies and was strongly correlated with initial seed weight. Biomass allocation patterns were significantly different among subspecies but not related to reproductive mode, seed weight or elevation or distance from the coast (of seed collection site). Leaf characteristics were associated with reproductive mode; the two semelparous subspecies had markedly higher estimated leaf areas than the other three taxa. All taxa increased allocation of biomass to corms under low moisture and high temperature "stress" conditions.

Yucca whipplei Torrey (Agavaceae) is an acaulescent, rosette-forming shrub distributed throughout semi-arid parts of southern and central California. This species has a number of distinctive floral and fruit characteristics that have led some authors to suggest its removal from the genus *Yucca* (McKelvey 1947). One characteristic unique among yuccas is *Y. whipplei*'s semelparous (monocarpic) life history; a rosette of stiff-tipped leaves grows vegetatively for some unknown number of years until a single flower stalk is produced, and then the entire plant dies within months of fruiting.

The semelparous condition is not found in all populations of *Y. whipplei.* Haines (1941) suggested five subspecies based on more or less geographically contiguous populations of differing reproduction or growth form. *Yucca whipplei* subsp. *whipplei* (subsp. *typica* of Haines) and subsp. *parishii* are the only semelparous taxa and are largely distinguished from each other by size. Subspecies *caespitosa* is an iteroparous perennial that produces multiple tightly packed

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rosettes (few to >100) from axillary buds early in development. These are all attached to a small caudex and the individual rosettes are homologous to branches that die after flowering. Subspecies *percursa* is a semelparous taxon that reproduces vegetatively by underground rhizomes that may extend several meters, often producing large dense colonies. A taxon with characteristics of subspp. *caespitosa* and *percursa* is subsp. *intermedia.* Although the subspecific designations of Haines (1941) are generally useful and are maintained in local floras, the growth form characteristics described by him for each taxon represent the most common condition throughout the regions attributed to each subspecies. Hoover (1973) pointed out that populations often consist of a mixture of reproductive modes (monocarpic, caespitose, or rhizomatous). For example, often 5% of the individuals in populations of subsp. *whipplei* actually produce more than a single rosette (J. Keeley, pers. obs.).

Subspecies of *Yucca whipplei* occupy a diversity of habitats. The semelparous subspp. *whipplei* and *parishii* are typically closely associated with chaparral, and the best developed populations are in the interior transverse and peninsular ranges. The iteroparous subsp. *caespitosa* is best developed in desert scrub vegetation bordering chaparral. The rhizomatous subsp. *percursa* commonly forms dense colonies on bare, rocky slopes and both this taxon and the coastal sage scrub subsp. *intermedia* are the most typically coastal subspecies.

The array of life history types represented in *Yucca whipplei* raises questions as to their origin and adaptive significance. Certainly seed germination and early seedling growth are critical stages that could be under different selective pressures across the *Yucca whipplei* range and may have some bearing on the different reproductive modes. The purpose of this study was to determine through garden experiments whether or not there are genetically based differences in seed germination and early seedling growth characteristics among these five taxa.

METHODS

Seeds were collected in 1978 and 1979 from five individuals in three widely separate populations of each subspecies. Air dry seed weights were taken for a sample of 100 seeds per subspecies.

Prior to germination experiments, seeds were stratified in plastic bags with a weak solution of fungicide (Dithane) and stored at 2°C for 4 weeks during early 1980. Germination was carried out on moist filter paper in plastic petri dishes maintained in the dark and scored after two weeks. Two germination experiments were performed. In the first experiment germination was compared between incubation at 25°C and 40°C for 1978 and 1979 seeds separately. Each treatment consisted of 10 petri dishes (each with 30 seeds) per population for a total of 30 dishes per subspecies. In the second experiment all seeds were incubated at 25°C, but prior to stratification and wetting, one set was heat treated in a convection oven at 110°C for 5 min and another set at 130°C for 5 min. Five dishes per population were used for a total of 15 per subspecies.

Seedling growth and biomass allocation patterns were examined as follows. Seeds were stratified as described above and planted (7 per pot) in 100 mm square pots ~10 mm below the surface of a 50/50 mix of washed sand and coarse grade perlite. Twenty pots were started for each of the three populations of each subspecies for a total of 60 pots for a control group and 60 pots for a "stressed" group as described below. Seeds were planted in early spring in an outdoor lathhouse with supplemental fluorescent lighting but covered with clear plastic to prevent moisture input from precipitation. The control group was fertilized weekly with commercial MiracleGro and maintained at field capacity soil moisture. The "stressed" group had elevated soil temperatures maintained by placing the pots 2 cm deep in sand with 37°C heating cables, fertilized monthly, and allowed to dry to the touch before rewatering. One month after planting each pot was thinned to four seedlings. After four months the largest seedling in each pot was collected and the number of leaves and length and width at the middle of the longest leaf were recorded. Leaves are linear and so leaf area was estimated by assuming each leaf approximated a rectangle. Each seedling was divided into roots, corms, and leaves, oven dried and weighed.

Data was analyzed by one-way ANOVA and Pearson product moment correlation.

Results and Discussion

There was no significant difference in germination behavior between 1978 and 1979 seeds, therefore, data for both years were combined. Under nearly all conditions, subsp. *parishii* with the heaviest seeds had the highest germination (Table 1) and subsp. *percursa* with the lightest seeds had the lowest germination. All taxa showed a marked reduction in germination when incubated at 40°C (Table 1). Even though some subspecies came from desert sites and others from coastal sites, there was no significant difference in germination at 40°C. Although several of the taxa are restricted to fire-prone environments, there was no indication that heat shock provided any sort of germination cue (Table 2), as is the case in many other chaparral shrubs. This is consistent with the observation that, unlike most chaparral shrubs, *Y. whipplei* populations have an uneven age structure, with seedling recruitment in all aged stands, wherever appropriate openings in the canopy exist (J. Keeley, pers. obs.). However, the two subspecies restricted to chaparral (*whipplei* and *parishii*) showed the least reduction in germination at 110°C.

Table 1. Percent Germination of *Yucca whipplei* Subspecies Incubated at 25°C and 40°C, n = 60 Dishes of 30 Seeds (seed weights in mg are given in parentheses).

Subspecies	Seed weight $\bar{x} \pm SD$	25°C $\bar{x} \pm SD$	40°C $\bar{x} \pm SD$	p
whipplei	(17.6 ± 4.9)	48 ± 26	2 ± 6	<0.01
parishii	(21.3 ± 7.3)	72 ± 25	12 ± 16	<0.01
caespitosa	(18.1 ± 4.6)	57 ± 28	11 ± 14	<0.01
intermedia	(18.0 ± 3.7)	49 ± 29	6 ± 14	<0.01
percursa	(16.0 ± 4.3)	41 ± 27	8 ± 12	<0.01
p	<0.01	<0.01	NS	

Seedling biomass after four months showed highly significant differences among subspecies for all characters examined (Table 3). Sample sizes smaller than 60 reflect mortality; survival of the semelparous subsp. *whipplei* was least affected by stressed conditions, but stress greatly reduced survival of the rhizomatous subsp. *percursa*. There was a significant reduction in total biomass under stressed conditions for all subspecies. Stressed conditions did not alter the allocation of biomass to leaves for any of the subspecies, but all taxa allocated significantly more biomass to corms. Stressed conditions significantly reduced the number of leaves and thus the total estimated leaf area for all subspecies (Table 4). After four months of growth, the only seedling characteristic that was clearly associated with reproductive mode was the estimated total leaf area. Both semelparous taxa had markedly higher leaf areas than the other taxa.

Correlations of biomass characters (from Tables 3 and 4) with seed weight, elevation, and distance from the coast (of seed collection site) are shown in Table 5. Total biomass was most strongly correlated with seed weight. In addition populations from higher elevations and more interior sites tended to produce seedlings with greater biomass after four months growth. Most leaf characteristics were correlated with initial seed weight.

Table 2. Percent Germination of *Yucca whipplei* Subspecies in Response to Previous Heat Treatment of the Seeds Incubated at 25°C (n = 30 dishes of 30 seeds).

Subspecies	Control $\bar{x} \pm SD$	110°C/5 min $\bar{x} \pm SD$	130°C/5 min $\bar{x} \pm SD$	p
whipplei	39 ± 24	18 ± 22	0 ± 0	<0.01
parishii	55 ± 24	31 ± 22	8 ± 18	<0.01
caespitosa	48 ± 23	14 ± 20	1 ± 2	<0.01
intermedia	32 ± 21	9 ± 14	0 ± 0	<0.01
percursa	29 ± 21	6 ± 13	0 ± 0	<0.01
p	<0.01	<0.01	<0.01	

TABLE 3. BIOMASS AND ALLOCATION PATTERNS OF FOUR-MONTH-OLD SEEDLINGS OF *Yucca whipplei* SUBSPECIES MAINTAINED UNDER WELL-WATERED AMBIENT "CONTROL" CONDITIONS AND LOW MOISTURE HIGH TEMPERATURE "STRESSED" CONDITIONS. [a]Control vs. stressed comparisons were significantly different at $^{**}p < 0.01$, $^{*}p < 0.05$ or $p > 0.05$ if blank.

Subspecies	Biomass (mg ODW) Control $\bar{x} \pm$ SD (n)		Stressed $\bar{x} \pm$ SD (n)	% Leaves Control $\bar{x} \pm$ SD	Stressed $\bar{x} \pm$ SD	% Corms Control $\bar{x} \pm$ SD		Stressed $\bar{x} \pm$ SD	% Roots Control $\bar{x} \pm$ SD		Stressed $\bar{x} \pm$ SD
whipplei	1.1 ± 0.4 (54)	**[a]	0.8 ± 0.3 (54)	46 ± 12	44 ± 9	18 ± 7	**	22 ± 8	35 ± 10		34 ± 9
parishii	0.9 ± 0.5 (60)	*	0.7 ± 0.3 (35)	55 ± 11	53 ± 9	14 ± 6	**	18 ± 7	31 ± 11		29 ± 9
caespitosa	1.0 ± 0.4 (55)	**	0.7 ± 0.3 (48)	49 ± 12	50 ± 9	14 ± 4	**	19 ± 7	37 ± 11	**	31 ± 7
intermedia	0.8 ± 0.3 (56)	**	0.5 ± 0.2 (31)	52 ± 10	52 ± 8	16 ± 6	*	19 ± 5	33 ± 9	**	28 ± 6
percursa	0.7 ± 0.3 (48)	**	0.5 ± 0.2 (23)	57 ± 8	53 ± 9	15 ± 4	**	19 ± 6	28 ± 8		28 ± 6
p	<0.01		<0.01	<0.01	<0.01	<0.01		<0.01	<0.01		<0.01

TABLE 4. LEAF CHARACTERISTICS OF FOUR-MONTH-OLD SEEDLINGS OF *Yucca whipplei* SUBSPECIES MAINTAINED UNDER WELL-WATERED AMBIENT "CONTROL" CONDITIONS AND LOW MOISTURE HIGH TEMPERATURE "STRESSED" CONDITIONS. [a]Control vs. stressed comparisons were significantly different at $^{**}p < 0.01$, $^{*}p < 0.05$, or $p > 0.05$ if blank. [b]Leaf area was estimated by assuming each leaf approximated a rectangle and multiplying by the total number of leaves/plant.

Subspecies	Leaf width (mm) Control $\bar{x} \pm$ SD		Stressed $\bar{x} \pm$ SD	Leaf length (mm) Control $\bar{x} \pm$ SD		Stressed $\bar{x} \pm$ SD	No. of leaves Control $\bar{x} \pm$ SD		Stressed $\bar{x} \pm$ SD	Estimated total leaf area (cm^2)[b] Control $\bar{x} \pm$ SD		Stressed $\bar{x} \pm$ SD
whipplei	2.4 ± 0.5	**[a]	2.1 ± 0.7	14.0 ± 1.8		14.6 ± 1.9	4.4 ± 0.7	*	4.1 ± 0.7	14.5 ± 4.3	**	12.6 ± 5.8
parishii	2.6 ± 0.5	**	2.2 ± 0.7	13.5 ± 2.3		13.6 ± 2.3	3.9 ± 0.6	**	3.4 ± 0.6	14.1 ± 4.7	**	11.0 ± 6.4
caespitosa	2.3 ± 0.5		2.3 ± 0.9	13.2 ± 2.1		12.3 ± 1.8	3.9 ± 0.5	**	3.4 ± 0.5	12.1 ± 3.5	*	10.1 ± 5.9
intermedia	2.1 ± 0.6		2.1 ± 0.6	13.7 ± 1.8	*	14.6 ± 2.3	3.9 ± 0.7	**	3.3 ± 0.5	11.6 ± 3.3	**	9.5 ± 3.6
percursa	2.2 ± 0.5		1.9 ± 0.5	11.8 ± 2.0		12.6 ± 1.7	4.1 ± 0.1	**	3.4 ± 0.7	10.5 ± 3.5	*	8.3 ± 3.6
p	<0.01		<0.01	<0.01		<0.01	<0.01		<0.01	<0.01		<0.01

TABLE 5. CORRELATION OF SEED WEIGHT, ELEVATION AND DISTANCE FROM THE COAST OF SEED COLLECTION SITE WITH GROWTH CHARACTERISTICS OF FOUR-MONTH-OLD *Yucca whipplei* SUBSPECIES COMBINED (n = 273 for controls and n = 191 for stressed plants). $^{*}p < 0.05$, $^{**}p < 0.01$, dash indicates no significant correlation.

	Seed weight Control	Seed weight Stressed	Elevation Control	Elevation Stressed	Distance from coast Control	Distance from coast Stressed
Total biomass	0.46**	0.41**	0.14**	0.22**	0.18**	0.19**
Percent leaves	—	—	—	—	—	—
Percent corms	—	—	—	—	−0.17*	—
Percent roots	—	—	0.15*	0.15*	—	—
Leaf width	0.39**	0.36**	—	0.25**	0.30**	0.22**
Leaf length	0.21**	0.25**	—	—	—	—
Number of leaves	—	0.23**	—	—	—	—

In summary, *Yucca whipplei* exhibits significant ecotypic differentiation in seed germination and early seedling growth characteristics. Although there were highly significant differences among subspecies in biomass allocation patterns, these were not related to reproductive mode, elevation, or distance from the coast. It is unknown whether these population differences were selected by localized environmental differences or reflect genetic drift in populations that are often isolated from one another by considerable distances. Some patterns were similar among all taxa and undoubtedly reflect similar selective influences. For example all subspecies responded to low moisture and high temperature stress conditions in allocating more biomass to corms, possibly reflecting the fact that all are distributed in habitats or microhabitats subject to unpredictable droughts. Total biomass of seedlings after four months was also unrelated to reproductive mode. It tended to increase with elevation and distance from the coast and appears to be controlled by seed weight. The only clear association between reproductive mode and any of the other characters examined is in leaf characteristics. The two semelparous subspecies (*whipplei* and *parishii*), after four months growth in a common environment, had markedly higher total leaf areas than the other three taxa. Of the five *Yucca whipplei* subspecies, these two semelparous taxa are the ones most closely associated with the fire-prone chaparral. Larger leaf areas may allow for more rapid growth rates in subsequent years, a characteristic of selective value in habitats subject to frequent fires.

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